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Abstract

Human impacts have left and are leaving distinctive imprints in the geological record. Here we show that in North America, the human-caused changes evident in the mammalian fossil record since c. 14,000 years ago are as pronounced as earlier faunal changes that subdivide Cenozoic epochs into the North American Land Mammal Ages (NALMAs). Accordingly, we define two new North American Land Mammal Ages, the Santarosean and the Saintagustinean, which subdivide Holocene time and complete a biochronologic system that has proven extremely useful in dating terrestrial deposits and in revealing major features of faunal change through the past 66 million years. The new NALMAs highlight human-induced changes to the Earth system, and inform the debate on whether or not defining an Anthropocene epoch is justified, and if so, when it began.

Keywords

Anthropocene, biochronology, Holocene, land mammal ages, mammals, paleontology

Introduction

‘Anthropocene’ is an informal term now widely used to identify the time in Earth history that begins when *Homo sapiens* become a geological-scale force for planetary change (Crutzen, 2002; Steffen et al., 2011b; Zalasiewicz et al., 2012). Discussions are underway about whether to

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formally recognize the Anthropocene as a new geological epoch and where to place its beginning, but the debates are still unresolved (Crutzen and Steffen, 2003; Steffen et al., 2007, 2011a, 2011b; Waters et al., 2013). Many proponents of the Anthropocene suggest that it began either around the year AD 1800, coinciding with intensification of the Industrial Revolution and attendant changes to the Earth system, or else around 1950 when many geochemical, physical and biotic signals of human population growth and globalization accelerated and became evident worldwide (Crutzen and Steffen, 2003; Steffen et al., 2011a, 2011b; Zalasiewicz et al., 2012).

However, pronounced pre-18th century human influences on the global ecosystem also are evident in geological, archaeological and paleontological records. Geochemical signals arguably indicate human influence on the atmosphere as early as 8000 years ago (Ruddiman, 2003) (see also Crucifix et al., 2005, for arguments in opposition to this idea), and a large body of archaeological evidence documents humans as an integral part of the Earth system since their first appearance about 160,000 years ago. Such considerations have led some to recognize the 'Paleoanthropocene': the time from the first human impacts many millennia ago to the first widespread influence of industrialized society (Foley et al., 2014).

Among the pre-industrial anthropogenic impacts are step-wise changes in mammalian faunas around the world, characterized by the introduction and often extinction of species that accompanied human dispersal. On the global scale such events are diachronous, spanning hundreds of thousands of years. They correspond with dispersal of *Homo sapiens* out of Africa, to Eurasia and Australia, and finally to the Americas (Barnosky and Lindsey, 2010; Barnosky et al., 2004; Koch and Barnosky, 2006; Martin and Steadman, 1999; Martin and Wright, 1967; Wroe and Field, 2006). Within each continent and on islands, the human immigrations and their impacts on the non-human mammal species appear geologically rapid, resulting in pronounced faunal changes within as little as two millennia (Goebel et al., 2008; Koch and Barnosky, 2006; Meltzer, 2009; Waters and Stafford, 2007) and even within a century or so on some islands (Burney et al., 2001; Martin and Steadman, 1999; Steadman, 2006). Here we present evidence that these anthropogenically driven step-wise changes apparent in the fossil record of mammals provide a useful way to highlight some major human alterations to the Earth system that preceded industrialized Anthropocene times, while at the same time completing a formal biochronologic system that has proven valuable in subdividing geological time.

For pre-Holocene time, paleofaunal changes have been used to define biochronologic units known as land mammal ages. Land mammal ages subdivide geological epochs by recognizing distinctive assemblages of mammal species, each of which characterize a certain span of geological time (Figure 1). This is possible because at irregularly spaced intervals through the Cenozoic, the mammal fauna of a given place demonstrates marked species- and genus-level turnover caused by evolution, immigration and sometimes extinction (Woodburne, 2004b, 2006). These turnover events are rapid with respect to the relative coherency of species assemblages that persist from one turnover event to the next. Each coherent assemblage represents one land mammal age, and the relatively rapid turnover events result in recognizable boundaries that separate ages. Land mammal ages were first formalized in North America (Wood et al., 1941) and now are recognized to be 'one of the most useful ways with which to discuss the timing of geohistorical events' within a given geographic region (Woodburne, 2006). Subsequent to their definition in North America, land mammal ages were codified for South America (Flynn and Swisher, 1995), Asia (Wang et al., 2013) and Australia (Megirian et al., 2010). A method of subdividing time based on distinctive mammal faunas (the MN zones) also is widely used in Europe (Lindsay, 1997). As originally proposed, the North American Land Mammal Ages (NALMAs) subdivided the Paleocene through Pliocene epochs (Wood et al., 1941). Later, two NALMAs were defined to subdivide the

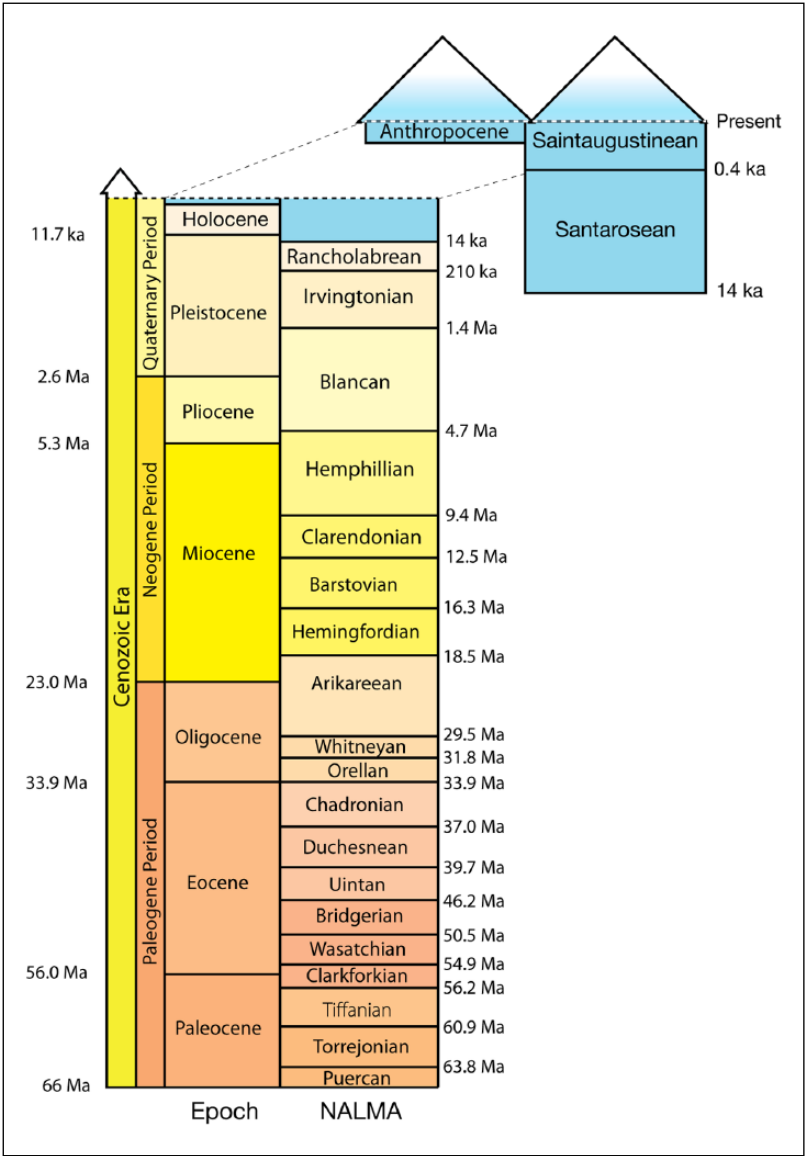


Figure 1. The North American Land Mammal Ages (NALMAs) and their correlation with the Cenozoic geologic timescale. The new NALMAs defined here are indicated in blue. ka = thousand years ago, Ma = million years ago.

Pleistocene (Savage, 1951), but the land mammal biochronology has, until now, excluded the Holocene (Figure 1).

Here, we complete this highly useful biochronologic scheme by defining two Holocene NALMAs, which serves two purposes. First, the new NALMAs enhance stratigraphic and temporal correlation in Holocene deposits that lack direct radiocarbon or other age determinations. Second, pertinent to the Anthropocene debate, recognizing Holocene NALMAs highlights the

important, step-wise episodes of human-induced ecological change that are otherwise hidden by the larger-scale Pleistocene–Holocene–Anthropocene trichotomy. Following standard practice of restricting land mammal age definitions to a given continent, the new land mammal ages apply only to North America. However, defining land mammal ages based on anthropogenically induced faunal changes, as we do for North America, is applicable worldwide (although temporal boundaries, characteristic taxa and names would by necessity differ for each continent).

The new NALMAs proposed here are the Santarosean, which begins with the first entry of humans into North America south of 55°N latitude, widely thought to have occurred between 14,000 and 15,000 years ago, and the younger Saintaugustinean, which begins with the introduction of domesticated megafauna north of 25°N latitude about 400 years ago. The beginning of the younger age (Saintaugustinean) defines the termination of the preceding NALMA (Santarosean).

Defining NALMAs

The North American Land Mammal Ages were first proposed (Wood et al., 1941) ‘to recognize discrete intervals of time based on the evolution of fossil mammals’ (Woodburne, 2004a); thus, the definition of a land mammal age is based solely on the mammal fauna as represented in the fossil record. As originally defined, the NALMAs were ‘only loosely tied to a stratigraphic framework’ (Woodburne, 2004a); this, and other nuances of the method by which NALMAs were first constructed (Woodburne, 2004b, 2006), means that, strictly speaking, they are biochronologic units. That is, NALMAs are ‘intervals of *time* [emphasis added] as represented by fossils’, rather than biostratigraphic units, which are empirical entities (physically, you can touch them) ‘based on stratigraphic disposition of fossils’ (Woodburne, 2004a). In this respect, NALMAs are similar to geochronologic units, the difference being that NALMAs were originally defined explicitly as time units that could be recognized from the evolutionary progression of mammal lineages, without specification of biostratigraphic zones first. That methodology differs from the normal procedure that a stratigrapher would have used, which is to first designate biostratigraphic zones, then use the time span of the biostratigraphic zone to recognize a material chronostratigraphic unit, the time span of which would be designated the geochronologic unit.

The definition of biochronologic units versus geochronologic ones may well reflect the prevailing interests of vertebrate paleontologists in understanding evolutionary relationships during the 1930s and 1940s, rather than emphasizing geological relationships, though of course, the two are in fact intimately intertwined – the initial NALMAs were defined in the midst of the Modern Evolutionary Synthesis. A decade later, the NALMAs that cover the last half of the Pleistocene (the older Irvingtonian and younger Rancholabrean; Figure 1) were defined (Savage, 1951). By that time, vertebrate paleontologists were explicitly grappling with how land mammal ages aligned with biostratigraphic units and, indeed, whether or not they were even biochronologic units (Savage, 1951).

It was later pointed out (Woodburne, 2004a, 2006), however, given that recognizing the evolutionary progression of fossil mammals relied on determining their distribution through strata, the land mammal ages were essentially grounded in biostratigraphic assemblage zones, although such zones were not specified. Subsequent work more rigorously characterized some of the NALMAs and portions thereof as formal biostratigraphic units by applying strict stratigraphic methodology (Woodburne, 2004a).

Current practice is still to regard land mammal ages as biochronologic units, although now first-appearance data are considered the best way to assign beginning and end points to the time intervals (Woodburne, 2004b, 2006). Thus, ideally, the beginning of each land mammal age is defined

by the first appearance of a single mammal taxon – either an immigrant or a newly evolved species – and the end of an age is defined at the beginning of the superjacent one. This approach is analogous to how biostratigraphic interval zones are defined; the difference being, with biostratigraphic interval zones, the defining taxa demarcate a physical entity, and with biochronologic units, the defining taxa demarcate the time that subsequent taxa first appeared. In defining a land mammal age, it is also customary to specify which taxa first appear within it (in addition to the boundary-defining taxon), which taxa go extinct and which genera or species are common in fossil deposits of that age.

It is important to recognize that, in the absence of independent dating to assign a numerical age to their boundaries, NALMAs indicate only the relative order of time slices, that is, which times were younger and which were older. Determining how old a given NALMA is – that is, when it begins and ends in terms of years before present – is a separate process from actually defining the NALMA, and relies on associating the fossils that document earliest records of the defining taxon with materials that can provide a numerical age-determination. The numerical dating is typically provided by radioisotopic techniques such as K-Ar, Ar-Ar, or magnetostratigraphy for older NALMAs, or U-series or radiocarbon dating for youngest NALMAs. Because the definition of the NALMA is decoupled from dating it, the numerical age of a NALMA can change without affecting its definition. Typically, such changes occur because new specimens of defining taxa are discovered and/or are associated with better numerical dates. In theory, it would be possible to fix boundaries at key localities and/or at agreed-upon dates (the ‘golden spike’ approach of designating a Global Boundary Stratotype Section and Point and/or Global Standard Stratigraphic Age), but such efforts have not yet been undertaken.

By convention (Savage, 1951; Wood et al., 1941; Woodburne, 2004a, 2004b, 2006), the name of a NALMA is derived from a geographic location that contains a particularly good example of a fossil assemblage characteristic of the age (notably, this is seldom the site that contains the first appearance of the defining taxon). See Woodburne (2006) for additional considerations and requirements, to which we adhere in defining the NALMAs presented here.

Santarosean North American Land Mammal Age

The name Santarosean is derived from Santa Rosa Island, California, where the Arlington Springs site has yielded some of the oldest directly dated human bones in North America (Erlandson et al., 2011; Goebel et al., 2008; Johnson et al., 2002; Waters and Stafford, 2007), domestic dogs *Canis lupus familiaris* (Rick et al., 2008) and taxa that last appear in this NALMA (*Mammuthus* and *Peromyscus nesodytes*) (Agenbroad, 2001; Rick et al., 2005, 2008). Santa Rosa Island was less separated from the mainland and contiguous with the adjacent Channel Islands when its earliest known humans arrived, because sea level was lower. As sea level rose, human occupation continued as the islands became disconnected from each other; the complex of archaeological sites on both Santa Rosa and the other Channel Islands records one of the most continuous sequences of human habitation from some 13,000 years ago into the latest Holocene. The archaeological evidence also is associated with fossils of terrestrial mammals, marine mammals and invertebrates (Erlandson et al., 2011; Rick et al., 2005), an association critical to correlating the newly defined NALMA to other biostratigraphic, geochronologic and archaeological timescales. This wealth of relevant data from the region makes Santa Rosa Island an ideal name-bearer for the newly defined land mammal age. Other sites (notably Anzick and Paisley Caves, see below), while candidates based on early occurrence of humans, exhibit a less rich suite and/or less continuous published record of associated taxa.

The beginning of the Santarosaeen NALMA is set at the earliest appearance of *Homo sapiens* in North America south of 55°N (Table 1). We follow standard practice for defining NALMAs by specifying a latitudinal boundary (Bell et al., 2004). Domestic dogs, *C. lupus familiaris*, also appear in North America first during the Santarosaeen (Morey and Wiant, 1992; Rick et al., 2008) (Table 1).

The beginning of the Santarosaeen – immigration of *Homo sapiens* into central North America – is well documented by many sites that contain unequivocal evidence of human presence associated with radiocarbon dates ranging from about 14.9 to 10.2 thousand years ago (Figure 2). (Throughout this paper radiocarbon dates are expressed in calendar years before present as calibrated using the Oxcal IntCal 13 curve.) The oldest well-substantiated dates on a human bone come from two sites. From one of them, the Anzick site in western Montana (Figure 2), an infant skeleton yielded an AMS ^{14}C date of 12,722–12,590 cal. yr BP (Rasmussen et al., 2014). The second date comes from Arlington Springs, which is located on Santa Rosa Island, California, the name-bearer for the new NALMA. Arlington Springs produced several human femur fragments (presumably from the same femur) that yielded dates ranging from 8982–8426 cal. yr BP (Johnson et al., 2002; Waters and Stafford, 2007) to 13,014–12,709 cal. yr BP (Erlandson et al., 2011; Goebel et al., 2008; Johnson et al., 2002). The oldest age-range is thought to be the most reliable because the bone fragment that yielded that date (13,014–12,709 cal. yr BP) was better preserved than other dated parts of the femur, and the femur was associated with a well preserved rodent jaw that produced a concordant date (Johnson et al., 2002) (and see Table 2).

The age determination for nearly all other early-human sites in North America relies on dating materials associated with archaeological evidence. Typically the dates are on charcoal, non-human bone, or wood that is found in stratigraphic proximity to human-made artifacts. Many of these dates cluster between about 12.6 and 13.0 thousand years old, and several are associated with Clovis artifacts (as is the Anzick infant), suggesting that the Clovis culture was widespread during an interval that lasted up to 400 years (Gilbert et al., 2008; Goebel et al., 2008; Meltzer, 2009; Waters and Stafford, 2007). The oldest dates that are widely accepted for human presence in central North America come from coprolites – purported to be human because they yield human as well as wolf ancient-DNA (Gilbert et al., 2008) – that were excavated from Paisley Caves, Oregon. These dates would place humans in Oregon by 14.1 thousand years ago, and possibly as early as 14.9 thousand years ago. Given that humans were certainly widespread in central North America by about 12.6 thousand years ago, and that Paisley Caves and other sites (Gilbert et al., 2008; Goebel et al., 2008; Meltzer, 2009) suggest pre-Clovis presence by at least 14,000 years ago, we provisionally set the beginning of the Santarosaeen at 14,000 years before present, recognizing that with more discoveries and dates, its inception may well be shown to be a few hundred years (or perhaps even more) older.

Extinctions of mammals within the Santarosaeen NALMA include many genera of megafauna and a few small-bodied mammal species. The megafaunal extinctions of at least 17 radiocarbon-dated genera occur between the time humans first entered central North America and approximately 10,000 years ago (Barnosky et al., 2004; Grayson, 2007; Koch and Barnosky, 2006) (Table 1). Therefore it is possible to recognize an early and a late phase for the Santarosaeen; the early phase is characterized by the co-occurrence of *Homo sapiens* with now-extinct megafauna of the genera *Arctodus* (short-faced bear), *Bootherium* (Harlan's musk ox), *Camelops* (camel), *Castoroides* (giant beaver), *Cervalces* (stag moose), *Equus* (native North American horse), *Euceratherium* (shrub ox), *Paramylodon* (ground sloth; earlier taxonomies consider this *Glossotherium*), *Mammuthus* (mammoth), *Megalonyx* (Jefferson's ground sloth), *Mylohyus* (Long-nosed peccary), *Nothrotheriops* (Shasta ground sloth), *Palaeolama* (stout-legged llama), *Platygonus*

Table 1. Newly defined North American Land Mammal Ages (NALMAs). The taxa listed under 'Common mammal taxa' are not exhaustive; only some very common representative genera are listed. In general, see Tables 2–5 for details and references.

	NALMA		
	Santarosean		Saintaugustinean
	Early	Late	
Start date	14 kya	10 kya	AD 1540
Defining taxa	<i>Homo sapiens</i>	<i>Homo sapiens</i>	<i>Equus caballus</i>
First appearances	<i>Homo sapiens</i>	<i>Canis familiaris</i>	<i>Bos taurus</i> , <i>Capra hircus</i> , <i>Felis catus</i> , <i>Mus musculus</i> , <i>Myocastor coypus</i> , <i>Oryctolagus cuniculus</i> , <i>Ovis aries</i> , <i>Rattus norvegicus</i> , <i>Rattus rattus</i> , <i>Sus scrofa</i>
Common mammal taxa	Extinct megafauna such as <i>Camelops</i> , <i>Equus</i> , <i>Mammuthus</i> , <i>Mammut</i> , giant ground sloths, etc. Extant taxa such as <i>Lepus</i> , <i>Microtus</i> , <i>Neotoma</i> , <i>Odocoileus</i> , <i>Sylvilagus</i>	Extinct megafauna absent. Many extant native North American taxa such as: <i>Canis</i> , <i>Castor</i> , <i>Cervus</i> , <i>Homo</i> , <i>Lepus</i> , <i>Microtus</i> , <i>Neotoma</i> , <i>Peromyscus</i> , <i>Odocoileus</i> , <i>Spermophilus</i> , <i>Sylvilagus</i> , etc.	Same as for Late Santarosean
Last appearances	* <i>Arctodus</i> , * <i>Bootherium</i> , <i>Bretzia</i> , * <i>Camelops</i> , § <i>Capromeryx</i> , * <i>Castoroides</i> , * <i>Cervalces</i> , * <i>Equus</i> , § <i>Eremotherium</i> , ¶ <i>Euceratherium</i> , § <i>Glyptotherium</i> , § <i>Hemiauchenia</i> , * <i>Mammut</i> , * <i>Mammuthus</i> , § <i>Megalonix</i> , § <i>Miracinonyx</i> , * <i>Mylohyus</i> , § <i>Navahoceras</i> , <i>Neochoerus</i> , * <i>Nothrotheriops</i> , <i>Oreamnos harringtoni</i> , * <i>Palaeolama</i> , § <i>Pampatherium</i> , * <i>Panthera</i> , * <i>Paramylodon</i> , * <i>Platygonus</i> , <i>Saiga</i> , * <i>Smilodon</i> , § <i>Stockoceros</i> , * <i>Symbos</i> , * <i>Tapirus</i> , § <i>Tetrameryx</i> , <i>Torontoceros</i> , § <i>Tremartctos</i>	<i>Ochotona whartoni</i> , <i>Peromyscus nesodytes</i>	<i>Canis rufus</i> , <i>Dipodomys gravipes</i> , <i>Geomys pinetis goffi</i> , <i>Microtus ochrogaster ludovicianus</i> , <i>Monachus tropicalis</i> , <i>Mustela nigripes</i> , <i>Neotoma anthoni</i> , <i>Neotoma bunker</i> , <i>Neotoma martinensis</i> , <i>Neovison macrodon</i> , <i>Peromyscus pambertoni</i> , <i>Peromyscus polionotus decoloratus</i> , <i>Peromyscus alticolus alticolus</i> , <i>Puma yagouaroundi</i> , <i>Sigmodon arizonae arizonae</i> , <i>Sigmodon fulviventris goldmani</i> , <i>Sorex ornatus juncensis</i>

Notes: For last appearances in the early Santarosean:

*Indicates genera for which robust radiocarbon dates indicate last records between 14 and 10 kya.

§Indicates genera for which radiocarbon dates have a reasonable probability of being older than 14,000 years, that is, the 95.4% probability range for calibrated dates extends beyond, or the entire range is older than, 14,000 years.

¶Indicates genera that have produced calibrated dates for which the 95.4% probability range extends younger than 10,000 years.

Genera without symbols do not have well-substantiated published radiocarbon dates.

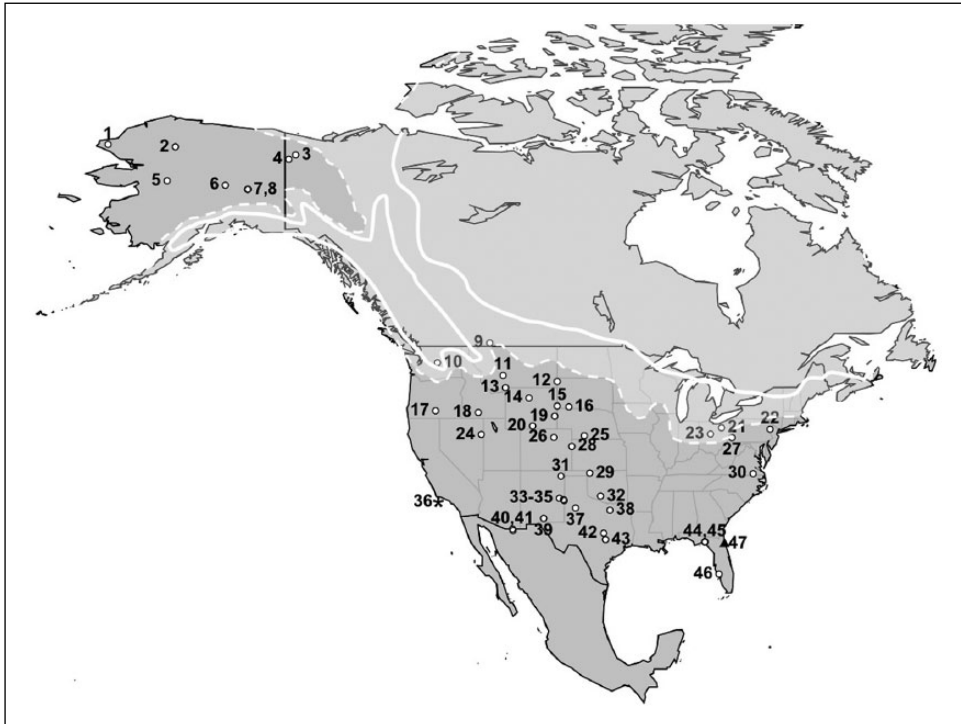


Figure 2. Map of North America showing localities relevant to the establishment of the new NALMAs. White dots indicate sites that document human presence between 14.9 to 10.2 thousand years ago. The * indicates Arlington Springs on Santa Rosa Island, namesake locality for the Santarosean NALMA; the Δ indicates Saint Augustine, Florida, namesake locality for the Santaugustinean NALMA. Lighter gray indicates area covered by glacial ice at the height of the last glacial (dotted white line), and at about 14,000 years ago when the Santarosean commenced (solid white lines). 1: Tuluq, AK; 2: Mesa, AK; 3: Old Crow, Canada; 4: Bluefish Caves, Canada; 5: Nogahabara, AK; 6: Nenana, AK; 7: Swan point, AK; 8: Broken Mammoth, AK; 9: Wally's Beach, Canada; 10: East Wenatchee, WA; 11: Indian Creek, MT; 12: Mill Iron MT; 13: Anzick, MT; 14: Colby, WY; 15: Sheaman WY; 16: Lange-Ferguson, SD; 17: Paisley Caves, OR; 18: Buhl, ID; 19: Hell Gap WY; 20: Union Pacific, WY; 21: Paleo Crossing, OH; 22: Shawnee-Minisink, PA; 23: Sheriden Cave, OH; 24: Bonneville Estates, NV; 25: La Sena and Lovewell, NE; 26: Dent, CO; 27: Meadowcroft, PA; 28: Kanorado, KS; 29: Jake Bluff, OK; 30: Cactus Hill, VA; 31: Folsom, NM; 32: Domebo, OK; 33: Clovis, NM; 34: Blackwater Draw, NM; 35: Arch Lake, NM; 36: Arlington Springs, CA; 37: Lubbock Lake, TX; 38: Aubrey TX; 39: Pendejo Cave, NM; 40: Murray Springs, AZ; 41: Lehner, AZ; 42: Gault, TX; 43: Wilson-Leonard, TX; 44: Sloth Hole, FL; 45: Page-Ladson, FL; 46: Warm Mineral Springs, FL; 47: Saint Augustine, FL.

(flat-headed peccary), *Smilodon* (saber-tooth cat), and *Tapirus* (tapir). Of those, all but *Bootherium*, *Mylohyus*, *Nothrotheriops*, *Cervalces* and *Casteroides* have been reported to be associated with evidence of humans in archaeological sites, though the strength of association in some cases is uncertain (Boulanger and Lyman, 2014; Grayson and Meltzer, 2002, 2003). Other megafauna taxa listed in Table 1 either have youngest radiocarbon dates that are older than 14,000 years, or have not produced dates. It is unknown whether those taxa were present when the first humans entered North America; more radiocarbon dates are needed to determine this. The available radiocarbon dates indicate that the early phase of the Santarosean spans from at least 14,000 (and probably

Table 2. Radiocarbon dates pertinent to establishing earliest human presence at Arlington Springs, Santa Rosa Island.

Material dated/stratigraphic context	C ¹⁴ age	Plus/minus	IntCal 13 calibration	Source
Femur fragment (A) CAMS-13055	7830	110	8982–8426	(Johnson et al., 2002)
Femur fragment (A) CAMS-16814	9180	70	10,520–10,225	(Johnson et al., 2002)
Femur fragment (B) CAMS-16810	10,960	80	13,014–12,709	(Johnson et al., 2002)
Charcoal from same stratum as human bone (CAMS-13036)	10,090	70	11,989–11,345	(Johnson et al., 2002)
<i>Peromyscus nesodytes</i> mandible from soil matrix around human femora (CAMS-17125)	11,490	70	13,468–13,181	(Johnson et al., 2002)
Soil layer above human bone	not reported	not reported	~12,900 (?)	(Johnson et al., 2007)
Upstream alluvial deposits thought to correlate with human bone-bearing layer	10,860	70	12,917–12,666	(Johnson et al., 2007)
Charcoal from organic earth in contact with human bone (L-568-A)	10,400	2000	19,780–7843	(Orr, 1960, 1962a, 1962b)
Charcoal from 1 foot away (L-650)	10,000	200	12,250–11,079	(Olson and Broecker, 1961; Orr, 1962a, 1962b)
Long bone fragment (UCLA-1899)	10,080	810	13,650–9551	(Berger and Protsch, 1989)
Charcoal from stratum beneath that in which human bone was found (UCLA-748)	11,300	160	13,452–12,814	(Berger and Libby, 1966)

Notes: Johnson et al. (2002) reviewed the radiocarbon dates that have been cited for establishing earliest human presence at Arlington Springs and reported those listed in the first five rows of this table. Dates obtained in the 1960s and 1980s are less reliable than those obtained in the Johnson et al. (2002) study because of improvements in analytical technique; in addition, the dates obtained in the 1960s and 1980s are from materials associated with human occupation, rather than from human bones (an exception might be UCLA-1899, though the taxon is not specified). Johnson et al. (2002) considered CAMS-16814 and CAMS-16810 to be the most reliable dates because they were on XAD-decalcified collagen. The differences in age, even though the samples come from the same femur, are due to differential preservation in different parts of the bone. The most ancient date on the femur (CAMS-17125) is concordant with one obtained from an even better preserved *Peromyscus* mandible (CAMS-17125) that was found in the same sediment block as the dated femur fragments. Meltzer (2009) noted that the human individual that was dated may have fed on marine organisms, which can skew a radiocarbon age; however, the agreement between the dates on human bones and the surrounding charcoal and *Peromyscus* bones suggests this source of error may not be significantly influencing the dates.

somewhat older, as noted above) to approximately 10,000 years ago (recognizing that additional radiocarbon dating efforts may well adjust the numerical age of this boundary). The late phase of the Santarosean is characterized by the occurrence of *Homo sapiens* but the absence of the extinct megafauna genera noted above. The late phase and the entire Santarosean NALMA terminates with the first appearance of domesticated megafauna in mid-latitude North America, which marks the beginning of the following NALMA, the Saintaugustinean.

Table 3. Summary of faunal information from 16th-century Saint Augustine. The table lists taxa represented by mammal bones found at archaeological sites. This information is based on excavations at six different sites: Lorenzo Joseph De Leon (SA 23-1), Lester's Gallery (SA 29-2), Episcopal Church (SA 31-1), Ximenez-Fatio (SA 34-2), Public Library site (SA 34-3) and Francisco Ponce de Leon (SA 36-4). (Reitz and Scarry, 1985).

Taxa	Lorenzo Jose De Leon	Lester's Gallery	Episcopal Church	Ximenez-Fatio	Public Library site	Francisco Ponce de Leon
<i>Bos taurus</i>	x	x	x	x	x	x
<i>Canis familiaris</i>	x					
<i>Capra/Ovis</i>	x					
<i>Didelphis virginiana</i>	x		x			
<i>Felis domesticus</i>	x		x	x		x
<i>Odocoileus virginianus</i>	x	x	x	x		x
<i>Procyon lotor</i>	x		x	x		x
<i>Rattus rattus</i>	x		x		x	
<i>Scalopus aquaticus</i>				x		
<i>Sciurus spp.</i>	x					x
<i>Sigmodon hispidus</i>	x		x			
<i>Sus scrofa</i>	x	x	x	x	x	x
<i>Sylvilagus spp</i>	x	x	x		x	x

Notes: Pedro Menendez de Aviles founded Saint Augustine in 1565. The ship that departed from Spain, which he commanded, was noted to have: 'One hundred horses and mares, two hundred calves, four hundred swine, four hundred sheep and some goats, and all the other cattle and livestock that shall seem proper to you' (Solís de Merás, 1923). Horse bones are rare in these archaeological sites because they were not typically used for food. The only horse remains are horse hairs from the Francisco Ponce de Leon site (SA 36-4) reported in (Deagan, 1978). Deagan (1978), citing Eugene Lyon, also mentions the presence of horsehair sieves in a 16th-century household inventory. The most abundant domestic animals found in the archaeological assemblages were pigs. Sheep and goats were introduced when St. Augustine was founded, but their establishment was not successful because of environmental conditions and they are not common in archaeological faunal assemblages at this time (Reitz and Scarry, 1985). Sixteenth-century affiliation of the materials has been made based on two criteria: 'Deposits had to originate at or below the earliest occupation level at the site' and were associated with ceramics that predated 1600 (Deagan, 1978).

Saintaugustinean North American Land Mammal Age

The beginning of the Saintaugustinean NALMA is defined by the first immigration of domesticated horses, *Equus caballus*, north of Mexico (25°N latitude). Other first appearances in the Saintaugustinean include *Bos primigenius* (domesticated cow), *Capra hircus* (domesticated goat), *Ovis aries* (domesticated sheep), *Sus scrofa* (domesticated pig), *Rattus norvegicus* (Norway rat), *Mus musculus* (house mouse) and *Felis catus* (domesticated cats) (Table 1) (Arnade, 1961; Crosby, 2003). The namesake for the NALMA is Saint Augustine, Florida, where Spanish colonizers established a settlement in 1565 that continues to be occupied today (Deagan, 1978), and from which archaeological and historical records document most of the taxa noted above (Reitz, 1992) (Tables 3, 4). Characteristic taxa include the suite of species that are still extant today (Kays and Wilson, 2002). Extinctions during the Saintaugustinean include *Neotoma anthoni* (Anthony's wood rat), *Neotoma bunker* (Bunker's wood rat), *Neotoma martinensis* (San Martín Island wood rat), *Neovison macrodon* (sea mink) and *Peromyscus pembertoni* (Pemberton's deer mouse), among others (IUCN, 2014) (Tables 1, 5).

Domesticated *Equus caballus* is designated the defining taxon because of its widespread occurrence in the paleontological and archaeological record, and because it is morphologically

Table 4. Summary of faunal information from 17th-century Saint Augustine. The table lists taxa represented by mammal bones found at archaeological sites. This information is based on excavations at two different sites: Ximenez-Fatio (SA 34-2), Public Library site (SA 34-3) and Francisco Ponce de Leon (SA 36-4) (Reitz, 1992). The two sites excavated here are the same sites studied for the 16th-century under the same name.

Taxa	Ximenez-Fatio	Francisco Ponce de Leon
<i>Bos taurus</i>	x	x
Caprine, Sheep/Goat	x	
<i>Equus caballus</i>		x
<i>Odocoileus virginianus</i>		x
<i>Procyon lotor</i>	x	
<i>Rattus</i>	x	
<i>Scalopus aquaticus</i>	x	
<i>Sciurus niger</i>	x	
<i>Sus scrofa</i>	x	x
<i>Sylvilagus palustris</i>	x	
<i>Sylvilagus</i> spp.	x	x
<i>Urocyon cinereoargenteus</i>		x

Notes: By the 17th century cattle ranches were established at St. Augustine and surrounding areas (Arnade, 1961). Reitz (1992) mentioned that horses and caprines were raised in the town or in nearby areas, but to a limited extent. Horses were a mark of status and their remains would be rare in midden deposits (Bushnell, 1981). *Ovis aries* and *Capra hircus*: Sheep and goats are difficult to identify from each other from their bone remains and usually are listed just as Caprine.

distinguishable from native North American Pleistocene horses (e.g. those that went extinct in the early Santarosaeen) through characteristics of the mandible, cranium and in some cases tooth wear associated with biting a bit (Figure 3). The introduction of domestic *Equus caballus* into the Americas is well documented through historical records that date the beginning of the Santaugustinean NALMA fairly precisely. By 1494, Spanish explorers had off-loaded horses onto islands in the Caribbean (Johnson, 1943), and by 1519, 16 horses had been ridden to the present site of Mexico City (Robinson, 2004). In 1539, the DeSoto expedition took 223 horses from Florida to Mississippi, and in 1540 the Coronado expedition, with their horses and other domesticated stock, penetrated into northern Mexico, Arizona and New Mexico (Chard, 1940; Haines, 1938; McKnight, 1959; Winship et al., 1896). This is the earliest documented introduction of domesticated horses that established a lasting breeding stock north of 25°N latitude; the horses, sheep and other domesticated animals the European explorers and colonizers introduced became incorporated into the lives of various Native American inhabitants. We therefore regard 1540 as the beginning of the Santaugustinean NALMA. Lasting populations of horses, sheep, goats and pigs were established in Saint Augustine, Florida, when it was settled in 1565 (Arnade, 1961; Deagan, 1978; Reitz, 1992) (Tables 3, 4), by which time domesticated horses were well established in northern Mexico and southwestern USA.

Implications of recognizing new NALMAs

Previously, the sequence of NALMAs ended with the Rancholabrean, which has generally been regarded as the time when the North American mammal fauna took on a modern aspect as indicated by the common occurrence of extant species (Bell et al., 2004; Savage, 1951). However, for about 95% of the Rancholabrean as previously defined, the fauna contained at least 60 extinct

Table 5. Species extinctions and extirpations in the Santaugustinean. Data from IUCN Red List of Threatened Species (IUCN, 2014).

Taxon	Date of extinction or extirpation	Global extinction species	Global extinction subspecies	Extirpated between 55° and 25° N latitude	Comment
<i>Canis rufus</i>	1980	Y			Re-introduced to North Carolina after going extinct in the wild
<i>Dipodomys gravipes</i>	1986	Y (possibly)			Listed as CR possibly extinct not seen since 1986 despite surveys
<i>Geomys pinetis goffi</i>	?		Y		
<i>Microtus ochrogaster ludovicianus</i>	?			Y	
<i>Monachus tropicalis</i>	1952	Y			
<i>Mustela nigripes</i>	1987			Y	Extinct in the wild 1987 – current pops are all re-introduced
<i>Neotoma anthonyi</i>	?	Y			No sightings since at least 2000
<i>Neotoma bunker</i>	?	Y			No sightings since at least 2000
<i>Neotoma martinensis</i>	?	Y			No sightings since at least 2000
<i>Neovison macrodon</i>	1894	Y			
<i>Peromyscus alticolus alticolus</i>	1930		Y		
<i>Peromyscus polionotus decoloratus</i>	?		Y		
<i>Peromyscus pemberton</i>	1931	Y			
<i>Puma yagouroundi</i>	?			Y	
<i>Sigmodon arizonae arizonae</i>	?		Y		
<i>Sigmodon fulvivent</i>	?		Y		
<i>goldmani</i>					
<i>Sorex ornatus juncensis</i>	?		Y		

megafauna species – most of them likely playing important roles in structuring regional and local ecosystems, as inferred from the ecological effects of extant large mammals (Estes et al., 2011; Owen-Smith, 1987) – and the species most characteristic of mammal faunas of modern aspect, *Homo sapiens*, was absent. Therefore, formally recognizing the Santarosean and Santaugustinean also gives the Rancholabrean coherency, by characterizing it as the last mammal faunas in North America that were not anthropogenically modified, rather than lumping the human-impacted faunas (Alroy, 2001; Koch and Barnosky, 2006) of the last temporal sliver of the Rancholabrean in with the pre-human faunas that comprise the vast majority of that NALMA. In addition, with definition of the more recent NALMAs discussed in this paper, the endpoint of the Rancholabrean becomes tightly placed at the immigration of a single taxon (*Homo sapiens*) into central North America, a procedure that conforms with the method used to define endpoints of all other NALMAs.

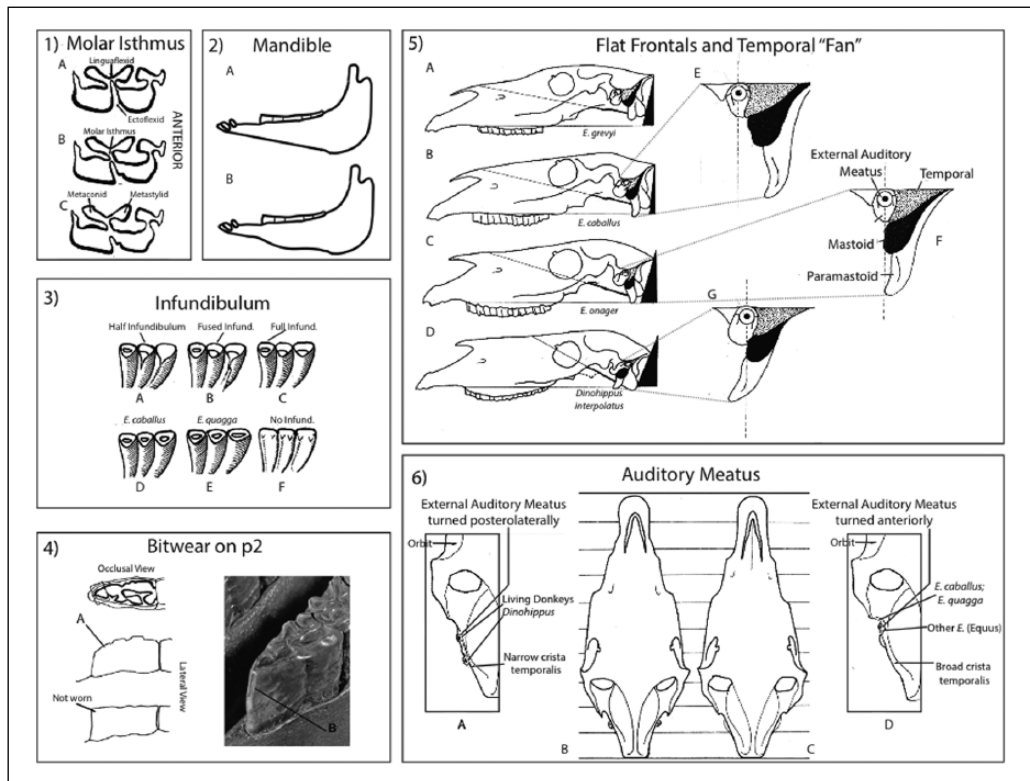


Figure 3. Morphological characters used to distinguish *Equus caballus* from Pleistocene *Equus*; drawings from Bennett (1980) and Brown and Anthony (1998). 1: A molar isthmus is present on the m3 in middle wear (A, B) and ectoflexids do not pass through it fully (C). 2: The mandible is relatively flat along the ventral borders of the horizontal rami (A) as opposed to dorsoventrally convex rami, with the deepest part of the jaw located ventral to the middle of the cheek tooth row as seen in Pleistocene *Equus* (B). 3: Full infundibulum in all lower incisors (D) and i3 is not elongate as seen in *E. quagga* (E). 4: Bitwear: p2 beveling – pitted and worn wear on the anterior 1/3 portion of the occlusal surface (see Brown and Anthony, 1998 and Anthony et al., 2006 for how to measure beveling); p2 anterior (nonocclusal) wear pattern (B), image from Scott et al. (2010). 5: Flat frontals across the dorsal surface (B) as opposed to frontal doming (A); Low basicranial flexion and small occipital angle (B) as opposed to high basicranial flexion and a large occipital angle (C, D); mastoid, paramastoid and temporal ‘fan’ is opened and mastoid has broad visible contact with the crista temporalis (E) as opposed to a closed ‘fan’ (G). 6: External auditory meatus turned anteriorly and close behind the glenoid (E) as opposed to angled posteriorly (A) as seen in living donkeys and *Dinohippus* or positioned posteriorly as seen in all other *E. (Equus)* (D); paramastoid processes and the mastoid portion of the temporal bone can be clearly observed in dorsal view lateral to the crista temporalis even though the crista temporalis is broadened (C). This differs from the external auditory meatus being visible in dorsal view due to narrow crista temporalis (B).

Until now, the Rancholabrean has had a diachronous and somewhat amorphous endpoint defined generally as at the extinction of the Pleistocene megafauna (Bell et al., 2004), which as presently known may span several thousand years in North America (Grayson, 2007; Grayson and Meltzer, 2003; Koch and Barnosky, 2006), although as noted above, the majority of well-dated last records of genera cluster between 14,000 and 10,000 years ago.

The two NALMAs we define here also underscore three step-wise changes in mammal faunas of North America that occurred since c. 14,000 years ago, each of which reflects increasing anthropogenic influence in ecological structuring. The first is at the inception of the Santarosean, when a new megafaunal species – *Homo sapiens* – immigrated into the North American ecosystem, influencing the ecological network in major ways as a large predator and omnivore (Alroy, 2001; Barnosky, 2008). The second major modification is the transition from the early to the late Santarosean, marked by the extinction of at least 17 megafaunal species. Most recent work attributes at least some of these extinctions to human influence, although the intensity of the event was probably also exacerbated by climate change (Brook and Barnosky, 2012; Koch and Barnosky, 2006). After this, human population sizes continued to grow, as humans became the primary megafaunal species on the continent. The beginning of the Saintaugustinean heralds the onset of yet another significant faunal event, with the addition of several new megafaunal species – this time large animals bred to serve human needs.

While we focus on North America in this study, an increasingly well documented paleontological and archaeological record worldwide indicates that this three-step progression is characteristic of how mammal faunas have evolved on all continents, although the timing of human arrival, megafaunal extinction, rising importance of domesticated megafauna and species involved differ in each case. These last three steps in development of the existing mammal fauna are equal in magnitude and character to pre-anthropogenic faunal changes, which form the basis for clearly demarcating successive episodes of Cenozoic time and subdividing geological epochs. Therefore, our results also bear on the ongoing debate regarding whether humans have introduced a geological and paleontological legacy to the extent that designation of an Anthropocene epoch is warranted. First, at least in the paleontological record of North American mammals, an anthropogenic legacy is already evident, which suggests that the even more intense human impacts since onset of the Industrial Revolution will trigger yet another step-wise change; indeed, historic extinctions of mammals in North America (Table 5) and increased extinction risks worldwide indicate those impacts already are underway (Schipper et al., 2008). Second, the past step-wise changes in the mammal paleontological record highlight that the Anthropocene as presently conceived (Steffen et al., 2011a; Waters et al., 2013; Zalasiewicz et al., 2012) had an important prelude: anthropogenically induced changes to the Earth system began long before human impacts intensified over the past two centuries (Foley et al., 2014). We suggest that recognizing this prelude is essential to inform discussions about whether the Anthropocene merits designation as a geological epoch, when the Anthropocene actually began (whether or not it attains formal epoch status), and how the biosphere has evolved as a result of human activities on Earth.

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